

A NEW SCLERACTINIAN-LIKE CORAL FROM THE ORDOVICIAN OF THE SOUTHERN UPLANDS, SCOTLAND

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ABSTRACT. New, discoidal fossils preserved as moulds from the middle Ordovician (Caradoc) of the Southern Uplands are shown to possess characteristic coralline microarchitecture. They are solitary, zoantharian corals with cyclic, hexamerl septal insertion. Successive cycles are arranged in a system of nested triads similar to patterns associated with septal substitution in scleractinian corals. The corallum lacks tabulae or dissepiments but is epithecate with the point of origin a basal disc as in Scleractinia rather than a cone as in Rugosa. The new coral is named *Kilbuchophyllum discoidea* gen. et sp. nov., and is placed in the new family Kilbuchophyllidae and the new order Kilbuchophyllida. It is interpreted as an early example of skeletal acquisition by the group of anemones that ultimately gave rise to the Scleractinia in the Middle Triassic. The phylogeny of the Zoantharia is briefly discussed in the light of this new material.

A STRIKING feature of the geological distribution of fossil corals is the sequential ranges of the two major and crudely homoeomorphic groups possessing well developed septa. The Rugosa appear in the mid-Ordovician and become extinct at the end of the Permian (Scrutton 1979, 1988; Hill 1981), whilst the Scleractinia first occur in the middle Triassic and persist to the present day (Wells 1956; Oliver 1980). No early Triassic corals are known. The fundamental distinction between these two groups of corals lies principally in their modes of septal insertion, serial in four quadrants in the Rugosa, and cyclic, hexamerl in the Scleractinia (Oliver 1980). Other zoantharian corals occur in the Palaeozoic but are less comparable. The small, enigmatic Devonian-Carboniferous order Hexacorallia is also strongly septate but distinct in septal pattern from both Rugosa and Scleractinia (Hill 1981). A third major group of exclusively Palaeozoic and colonial corals, the Tabulata, have variably and generally weakly developed septa for which no definite pattern of insertion has yet been established. Claimed rugosan insertion in *Agetohites* (Kim 1974) requires restudy before its significance can be assessed. In addition, pre-Ordovician beds have yielded a small number of coralline organisms, one of which, *Cothonion*, has well developed septa and may derive from the same stock as the Rugosa (Scrutton 1979; Jell 1984).

Although direct descent of the Scleractinia from the late Palaeozoic Rugosa has been claimed by Schindewolf (1942) and others, the alternative view that the Scleractinia evolved independently from anemone precursors in the middle Triassic has been strongly argued by Oliver (1980). Over the years, a number of Palaeozoic corals had been described as exhibiting scleractinian characters. However, Hill (1960) noted that 'all Palaeozoic corals claimed...to be Scleractinia have subsequently been proved to be Rugosa...'. The sole uncertainty she allowed was the record of apparent Permian age of species of the genus *Omphalophyllia* by Minato (1955). This Japanese material is too poorly preserved to be reliably interpreted and its restudy is required; Minato (1955, p.180) considered the possibility that it was related to *Lophocarinophyllum*. On the other hand, the host rock is now interpreted as an olistostrome in a Triassic accretionary complex containing Carboniferous, Permian and Triassic olistoliths; thus there are no positive data to support Permian *Omphalophyllia* (Makoto Kato pers. comm.). The type material of *Omphalophyllia* is a Triassic scleractinian coral, considered a synonym of *Conophyllia* by Wells (1956). Since then, the possibility of a scleractinian presence in the Palaeozoic has continued to be raised. Krasnov (1970) considered Scleractinia of fungiid type to have separated from the Rugosa in the early to mid Palaeozoic with

the Calostylidae as the most likely ancestral group. However, Smith (1930) had already shown *Calostylis* to have rugosan septal insertion and this was confirmed by Weyer (1973). More recently, Erina and Kim (1980) considered the Ordovician *Sumsarophyllum* and their new genus *Tjanshanophyllia* to both show fungiid characteristics on the basis of many cycles of perforate septa and the reported lack of an epitheca. They did not demonstrate cyclic, hexamerall septal insertion, however, which must be considered the critical evidence for rejecting classification with the Rugosa and supporting comparison with the Scleractinia. Oliver (1980) concluded at that time that no known Palaeozoic coral demonstrated cyclic septal insertion.

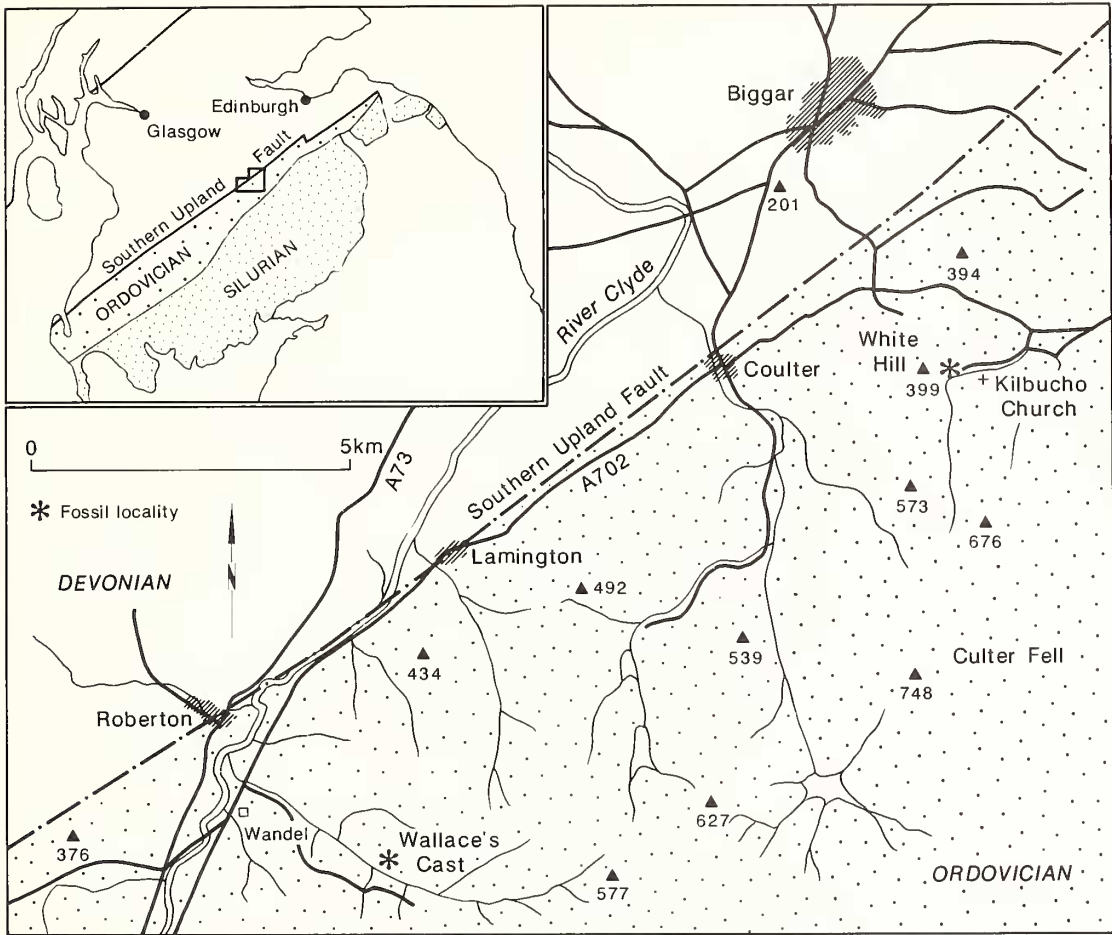
Thus we regard our description here of a new Ordovician solitary coral with scleractinian characteristics as the first well documented case of a Palaeozoic scleractiniomorph. Our claim is based on a full assessment of the structure and development of the coral, including and principally, the clear expression of hexamerall cyclic septal insertion. We presuppose our conclusions concerning the nature of this material and scleractinian coral terminology is used throughout for the morphological descriptions (Wells and Hill 1956).

Abbreviations. All material we have collected is housed in the Royal Museum of Scotland, Edinburgh (RMS). Additional material referred to is housed in the British Geological Survey, Edinburgh (BGS) and The Natural History Museum, Department of Zoology, London (BM(NH)Z).

FIELD OCCURRENCE

In the Southern Uplands of Scotland, Ordovician rocks extend as a continuous belt from the North Sea to the Irish Sea (Text-fig. 1). They are largely confined to the Northern Belt and consist in the main of Arenig volcanics overlain by a suite of younger sediments. The oldest sediments are Llanvirn-Llandeilu red and grey cherts; these are succeeded by black shales of Glenkiln age (*gracilis* and *peltifer* Zones), overlain in turn by Caradoc greywackes, grits and shales. Whereas all these sediments are typically of deep-water origin, there are a number of localities, referred to by Peach and Horne (1899), which have yielded shelly fossils. The best exposures are at Kilbucho (National Grid Reference NT 060338) and at Wallace's Cast in the Wandel Burn (NT 967263) (Text-fig. 1). Other occurrences were noted by Ritchie and Eckford (1935) westwards to Duntercleuch and Snar, North-west of Leadhills.

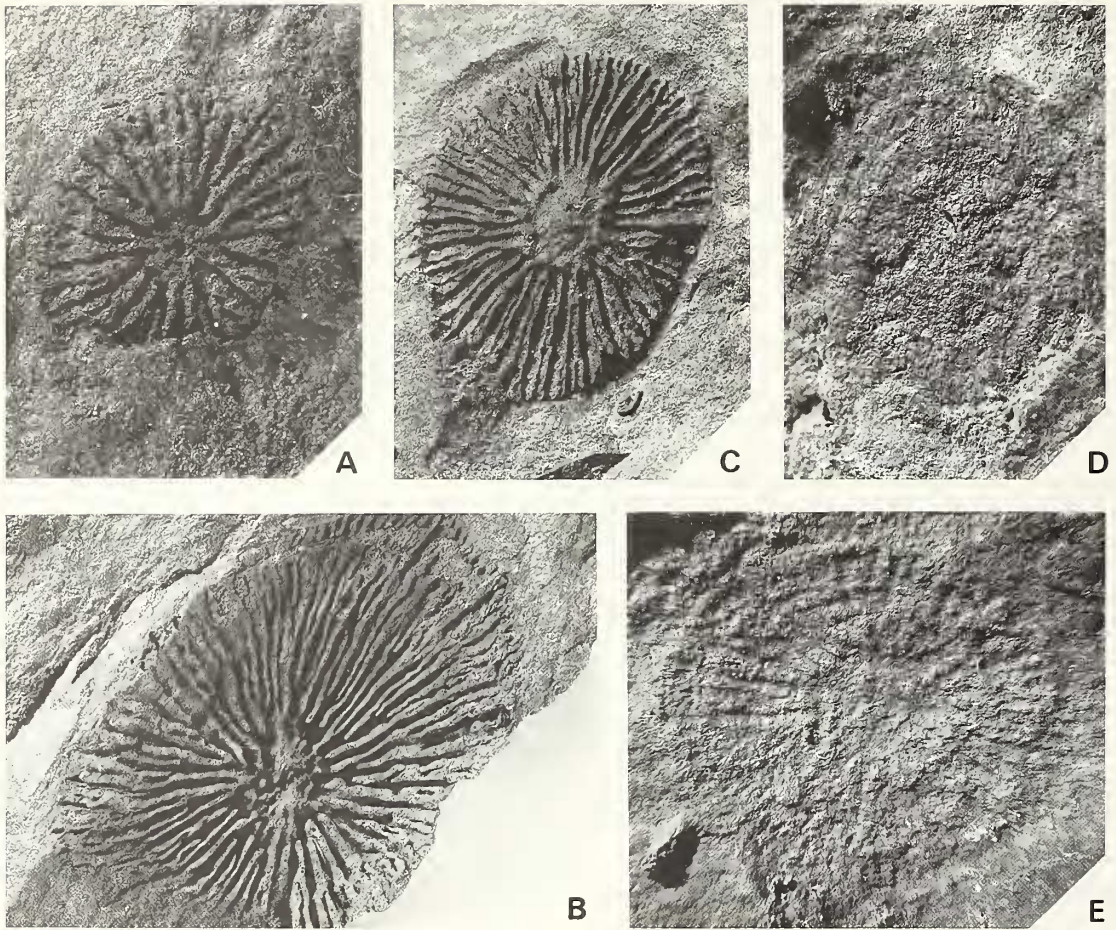
At Kilbucho and Wallace's Cast, imperfectly exposed though they are, basal greywackes are overlain by a coarse conglomerate with clasts of igneous rock, limestone and mudstone with undistorted fossils. This conglomerate fines upwards into siltstone turbidites and mudstones, cleaving subparallel with the bedding, which yield a rich assemblage of fossils, usually found in a rather distorted state. The total thickness of the conglomerates and associated siltstones and mudstones is no more than 5 m. These sediments are interpreted as debris-flow deposits, probably triggered seismically. They were originally laid down in shallow waters, following which, large unstable masses of partly and unlithified sediments slumped rapidly into deep-water, burying their faunas in the process. The sediments at the two localities of Kilbucho and the Wandel Burn are very similar, though they lie 12 km apart along the strike. It is quite possible that they record the events of a single debris flow of vast size although this cannot be confirmed. They could, on the other hand, have been smaller, separate, but near contemporaneous debris-flows from the same source. All the fossils are well-preserved as moulds (Text-fig. 2A-D), though distorted and not infrequently cracked, possibly during transportation or through diagenetic effects. The fossiliferous mudstones and siltstones are a classic obrution deposit, the fossils often being preserved at an angle to the bedding. A full description of the localities and other faunas is in preparation (Clarkson, Harper, Owen and Taylor in prep.). As well as a rich variety of brachiopods and trilobites, there are also bryozoans (especially common at Wallace's Cast), ostracodes, bivalves, gastropods, nautiloids and crinoids in addition to the material described here. Scattered solitary rugose corals are present at Wallace's Cast and rarely in mudstone clasts in the conglomerate at Kilbucho. The new genus described here



TEXT-FIG. 1. Map of the mid-north Southern Uplands of Scotland indicating collecting sites at Kilbucho and Wallace's Cast. Area of detailed map located in inset.

is known only from two poor fragments from Wallace's Cast but is common in a wide range of ontogenetic stages in a coarse-silt grade turbidite at Kilbucho, where it appears not to be associated with rugose corals.

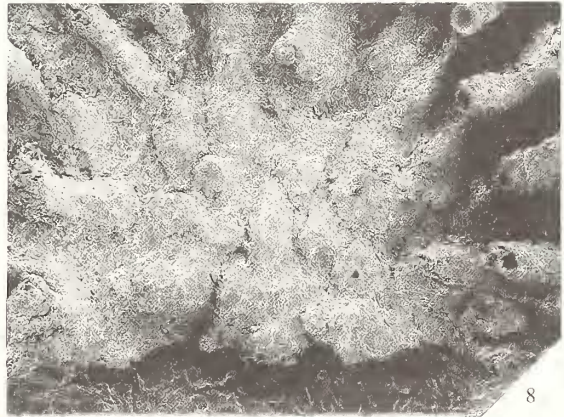
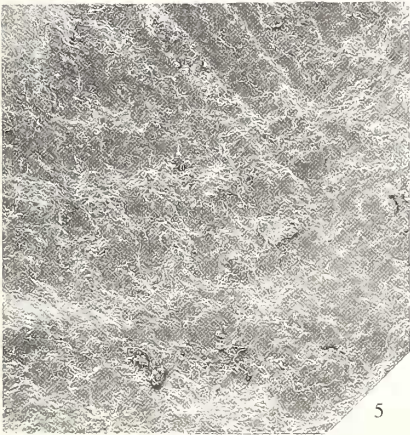
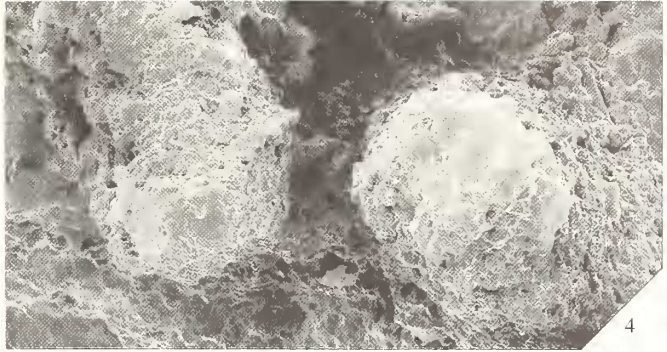
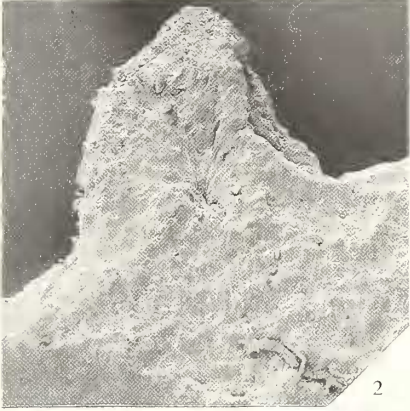
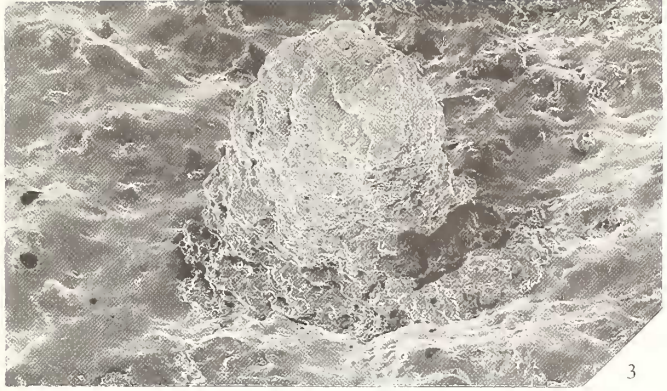
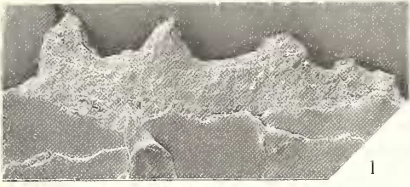
The graywacke group in which the Kilbucho-Wandel Burn sequence occurs lies within Tract 2 of the Southern Uplands (Leggett *et al.* 1979) and belongs to the Kirkcolm Formation (J. Floyd pers. comm.). The trilobite fauna is fairly diverse, there being twelve species (A. Owen pers. comm.), and there are up to twenty-four species of brachiopods (D. A. T. Harper pers. comm.). Amongst the trilobites, the most common faunal elements are the mid-Caradoc (Balclatchie and Ardwell) *Calyptraulax brongniartii* (Portlock) (see Clarkson and Tripp 1982) and *Iliaenus convergens*, with subsidiary *Stenopareia*, *Cybeloides*, *Paraharpes* and *Remopleurides*. The numerous brachiopods are very similar to those of the Bardahessiagh Formation, Pomeroy, Northern Ireland (Mitchell 1977), of high Ardwell age, but some of the elements are also found in the Balclatchie and Ardwell Beds at Girvan. The total age range of the Kilbucho-Wandel faunas cannot for the moment be dated more accurately than mid-Caradoc (Soudleyan - Actonian).



TEXT-FIG. 2. *Kilbuchophyllia discoidea* gen. et sp. nov. Ordovician, mid-Caradoc, Kilbucho, near Biggar, southern Scotland. A–D, original moulds; A, RMS 1989.36.2, calical surface of immature specimen in which septa are weakly linked spines (compare with Text-figs 3E, F); axis of symmetry vertical, $\times 5$; B, RMS 1989.36.1 (holotype), calical surface of mature specimen in which septa are solid blades (compare Text-fig. 3G, H); axis of symmetry vertical, $\times 2.5$; C and D, RMS 1989.36.7, calical surface; undersurface of epitheca, part and counterpart, $\times 3$. E, RMS 1989.36.8, latex replica of external surface of epitheca showing well developed interseptal grooves and growth ridges, $\times 4$.

EXPLANATION OF PLATE I

Figs 1–8. *Kilbuchophyllia discoidea* gen. et sp. nov.; all scanning electron micrographs of gold coated latex replicas; Ordovician, mid-Caradoc; Kilbucho, near Biggar, southern Scotland. 1 and 2, RMS 1989.36.4, mature septal blade, corallum axis to left; note pattern of diverging columnar units in fractured face in fig. 2; 1, $\times 15$; 2, $\times 60$. 3, RMS 1989.36.5, oblique view of individual trabecular spine set on internal surface of epitheca at peripheral margin of corallum, $\times 150$. 4, RMS 1989.36.2, plan view of pair of trabecular spines in mid septum, $\times 150$. 5 and 6, RMS 1989.36.6, external surface of epitheca, periphery of corallum bottom right; 5, general view showing prominent septal grooves and growth ridges, $\times 15$; 6, detail of growth ridge crossing interseptal ridge, $\times 45$. 7, RMS 1989.36.4, pattern of nested triads developed about third order septum in centre of figure; first order septum to left of group, second order septum to right of group, $\times 15$. 8, RMS 1989.36.5, papillose axial structure of merged trabecular spines, $\times 30$.



SCRUTTON and CLARKSON, *Kilbuchophyllia*

PREPARATION

The mouldic material, preserved in a coarse-silt grade, quartz-rich turbidite with a substantial mica and clay mineral matrix, was cleaned in a weak solution of Calgol in an ultrasonic bath and latex replicas were made using standard techniques. Although these replicas demonstrate overall three-dimensional appearance of the coral, distortion of the septal blades, either taphonomic or tectonic, tends to obscure the detailed interseptal relationships in most specimens. Therefore, septal patterns were traced directly from the moulds using a camera lucida attachment on the microscope. These reflect the growth of the septal blades on the upper surface of the epitheca and are thus likely to reflect the interseptal relationships most accurately. For the purposes of illustration in Text-figure 3, these patterns have been reversed to show the standard calical view of septal arrangement in corals.

The latex replicas were used for SEM study of septal microarchitecture. Selected replicas were coated with gold under vacuum to a thickness of 12–15 nm and examined at a range of magnifications using a Cambridge Instruments Stereoscan 240 in the Biomedical E.M. Unit at the University of Newcastle upon Tyne. Problems of creep in the latex were solved by working at low energy levels, between 0.5 and 4 kV. Very low magnification pictures taken at settings for maximum depth of field, such as that in Text-figure 3H, suffer from slight spherical distortion but have been preferred for their clarity over light microscope photographs.

In coral studies, mouldic preservation is usually regarded as of limited value. It is less of a disadvantage in the present material because of the discoidal growth form and lack of horizontal elements between the septa: no macrostructural detail is lost. However, the SEM results obtained here, suggest that all mouldic material may repay closer examination.

MORPHOLOGICAL CHARACTERISTICS

A full description of this new species is given below. The present discussion concentrates on the two most important features bearing on the anthozoan cnidarian nature of the material and its phylogenetic relationships within the class: microarchitecture of the skeletal elements and septal pattern.

Microarchitecture

SEM study of gold-coated latex replicas reveals the preservation of elements of about 20 μm and above in the better preserved material. Individual septal spines of up to 200 μm diameter, in specimens RMS 1989.36.2 and 5, are constructed of upward and outwardly diverging columnar units of indeterminate length and subrectangular to rhomboidal to irregular (?oblique) section, *c.* 20 μm across (Pl. 1, figs 3 and 4). Viewed from above, terminations give the appearance of overlapping roof tiles, possibly helically arranged in a conical stack. Where spines are first linked to form continuous but beaded septal plates, the intervening ridges are composed of units of similar size and shape. In larger coralla, in which individual spines have been subsumed into dentate, flat faced septal blades, the lateral faces of the blades have the appearance of a uniform fabric of overlapping scales (Pl. 1, figs 1 and 2). On the fractured surface of a septal tooth, internal upward fanning of columnar units is visible; the effect of overlapping scales is produced by oblique terminations of these units at the surface. No substructure is visible within these units.

The axial structure in some smaller coralla is composed of a cluster of discrete spines (Pl. 1, fig. 8). These have the same structure as the septal spines and are clearly septal in origin.

The basal surface of the epitheca shows circumferential ridges, demarcating growth increments, and sometimes, except in the axial area, radiating septal grooves (Pl. 1, fig. 5; Text-fig. 2D,E). In between ridges, the surface is smoother and may be very smooth to almost featureless. At the ridges, a cluster of overlapping triangular to arcuate elements averaging 40 μm across forms a low scarp slope directed towards the axis (Pl. 1, figs 5 and 6). Individual elements are oriented radially and offlap towards the periphery, the ultimate series in each ridge subparallel to the inter-ridge surface of the epitheca. The calicular surface of the epitheca is rather smooth and undulating in places but elsewhere shows sub-vertically orientated elements with low pyramidal terminations approximately 20–40 μm across. These define a fabric which appears to have a crudely radial orientation in places (Pl. 1, fig. 3).

Septal pattern

Septa are arranged radially, reaching up to 0·8 of the corallum radius in length, on a flat, circular (see below) basal disc. Pattern is most readily detected in the smaller coralla with about 30–40 septa. In larger, mature coralla, with up to 120 septa, not only are most specimens incomplete but septal arrangement becomes increasingly irregular.

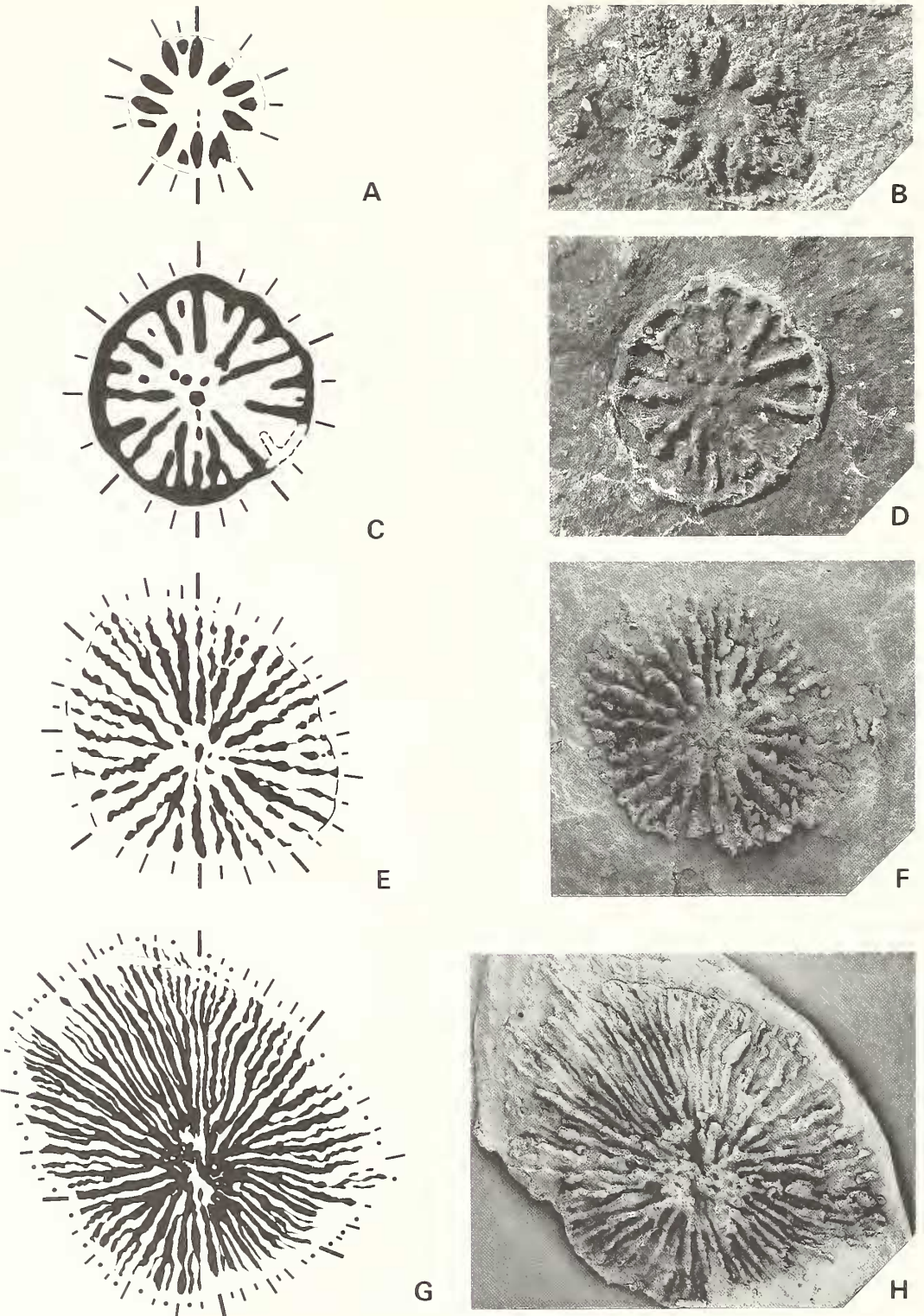
Two features reveal the septal pattern: the relative length of the septa, and curvature of the inner ends of septa of higher order to face, or rest against the flanks of septa of lower order (Pl. 1, fig. 7). In RMS 1989.36.2 (Text-figs 2A and 3E, F), 12 septa of approximately equal length extend 0·8 radius to the axis. Of these, alternate septa are each flanked by two shorter septa, between 0·5 and 0·75 radius in length, whose axial ends turn, more or less strongly, towards each other and the opposite faces of the dividing, longer septum. There are thus 12 of these shorter septa. Eight of these are again each flanked by a pair of even shorter septa, 0·1 to 0·5 radius in length and converging on opposite faces towards the axis. This repeated pattern of septal convergence leads to the appearance of nested triads of septa of which there are six, separated by six of the longest septa which have no divergent septal groups. These latter are interpreted as six first cycle septa, alternating with six second cycle septa that form the axis of each set of nested triads. The successive groups of diverging septa represent, respectively, 12 third cycle septa and 16 fourth cycle septa, amounting to 40 septa in all. The fourth cycle here is regarded as incomplete, numbering 24 septa when complete. The two triads lacking fourth cycle septa are adjacent and flank an axis of bilateral symmetry defined by a short septal blade in the axial area of the coral.

All of the available material, except the smallest specimen, clearly shows this septal pattern of nested triads and often some weak indication of an overall bilateral aspect. Two further specimens unequivocally, and several others less certainly, demonstrate the hexamerous symmetry of the pattern of triads. One, RMS 1989.36.4 (Pl. 1, fig. 7), is only slightly larger than RMS 1989.36.2 and shows complete first to fourth cycles of septa and an incomplete fifth cycle containing 10 septa. The pattern of nested triads is uncertain and probably anomalous in one sextant; the specimen is damaged at this point. A bilateral symmetry is suggested by the 5th cycle occurring almost exclusively in two opposite sextants. RMS 1989.36.1 (Text-fig. 3G, H) is close to the maximum diameter known so far for this coral. It also shows complete first to fourth cycles of septa, whilst the fifth cycle is better developed but still incomplete with 31 septa and the sixth cycle rarely developed and represented by 6 septa. Bilateral symmetry is again suggested by septal arrangement in and around the axial area and by slightly higher septal numbers in two opposite sextants. However, the numerical difference is small and peripheral preservation incomplete so that septal number may be higher than apparent.

Only two relatively immature specimens are available (Text-fig. 3A–D). No pattern of convergence is seen in the smallest specimen, RMS 1989.36.3 (Text-fig. 3A, B), and septal identity is uncertain: the interpretation shown draws on comparison with the pattern developed in larger coralla. The larger specimen shows weakly developed triads. We have been conservative in our interpretive sketch (Text-fig. 3C) and faint traces on the specimen suggest the possibility of greater axial extension of the third order septa towards the second order septa (Text-fig. 3D). The appearance of third order septa in more mature specimens suggests that some extension or strengthening of their axial ends takes place as growth proceeds.

The details of septal insertion cannot be substantiated by a study of septal grooves on the underside of the epitheca. These are only rarely well-developed and tend to fail almost completely in an axial area *c.* 4 mm across. Often the whole epitheca appears to lack septal grooves (Text-fig. 2D). Supporting evidence is limited to faint indications of peripheral triads, as at top-right in Text-figure 2E.

Many specimens show varying degrees of irregularity in insertion. However, an overall pattern emerges of a pair of adjacent sextants relatively retarded and a further pair of opposite sextants relatively accelerated. The pattern is symmetrical about the plane of bilateral symmetry where this is clear from features in the axial area of the corallum. In the smallest coralla available (Text-fig. 3A–D), retardation is already apparent in the adjacent pair of sextants (orientated towards the



TEXT-FIG. 3. For legend see opposite.

bottom of each figure). Acceleration in lateral sextants does not become marked until the insertion of the 5th cycle begins. It may be so extreme in some larger corallites that an initial impression is given of eight rather than six sets of nested triads. An idealized representation of the septal pattern in these corals is given in Text-figure 4A.

AFFINITIES AND RELATIONSHIPS

Anthozoan affinities

The gross morphological features of these specimens immediately suggest coralline affinity. The only other reasonable possibility seems to be a relationship to the Porifera, based on a crude homeomorphy with forms like *Haplistion* (Rigby 1987). No other phylum is known to produce a structure of this size range and form.

The microarchitecture of the septa clearly rules out poriferan affinity and strongly supports assignment to the Anthozoa Cnidaria. The characteristic pattern of elements in the septal spines can be matched very closely among the Scleractinia (for example, Sorauf 1972). In particular, the appearance of granulations on the lateral faces of septa in *Fungia*, representing one spherulitic cluster of crystallites (Sorauf 1972, pl. 14, fig. 5), is indistinguishable in appearance from the tips of the septal spines in the present material, although smaller in size (Pl. 1, figs 3 and 4). Granulations on the septal faces in *Cladocora* (Sorauf 1972, pl. 13, fig. 4) are also similar. The fabric on the lateral faces of septal blades (Pl. 1, figs 1 and 2) compares with that in *Fungia scutarea* (Sorauf 1972, pl. 11, fig. 2) but is much coarser. The elongate units defined in the present material are assumed to be composed of bundles of fine acicular crystals, not resolvable here either because of the limitations of the moulding medium, or recrystallization, or both. However, there seems to be sufficient evidence to establish the septal spines as trabeculate. Such microstructure appears to be characteristic of the anthozoan Cnidaria.

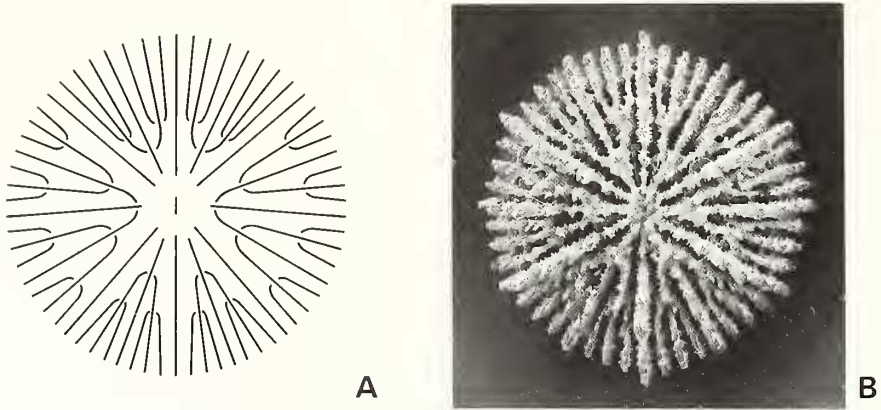
This evidence, together with the discoidal epithecate form and the radial distribution of the spinose or bladelike septa, clearly identifies this material as a zoantharian coral.

Affinities within the Anthozoa

In detail, this material is unlike any other known Palaeozoic coral, either from the established Rugosa or Heterocorallia, or the more scattered and problematic Cambrian material. It is grossly most similar to some solitary, discoidal Rugosa (for example, Hill 1981, fig. 39) but is fundamentally distinguished from them by its septal arrangement. These new specimens unequivocally show six-fold cyclic insertion in contrast to the serial insertion in four quadrants of rugose corals. The septal development in Hexacorallia, based on four primary septa (Hill 1981), is even more distinct. On the other hand, this pattern of cyclic insertion is indistinguishable from that in scleractinian corals (Vaughan and Wells 1943; Wells 1956; Jell 1980; Oliver 1980). The tendency for cycles, particularly above the third, to be incomplete when higher cycles are initiated is common in Scleractinia. The evidence of bilateral symmetry is also seen in septal development in many scleractinians and, as pointed out by Oliver (1980), is a reflection of the fundamental radiobilateral symmetry of all known anthozoans. A dorso-ventral polarity in the insertion of septal cycles is a feature of some scleractinians (Vaughan and Wells 1943; Wells 1956; Oliver 1980) and we interpret the relative retardation of a pair of sextants in the present material to indicate the equivalent of the ventral pole

TEXT-FIG. 3. *Kilbuchophyllia discoidea* gen. et sp. nov. Ontogenetic series, Ordovician, mid-Caradoc, Kilbucho, near Biggar, southern Scotland. Photographs (B and D) and scanning electron micrographs (F and H) of latex replicas of calical surfaces are matched with interpretive sketches based on information from original moulds and corresponding replicas. Plane of bilateral symmetry vertical, supposed dorsal pole at top. Septal cycle indicated as follows: protosepta, long heavy lines; 2nd, 3rd and 4th cycles, successively shorter light lines; 5th cycle, spots; 6th cycle, unornamented. A and B, RMS 1989.36.3, $\times 8$. C and D, BGS 9936, $\times 8$. E and F, RMS 1989.36.3, $\times 6$. G and H, RMS 1989.36.1 (holotype), $\times 2.5$.

in scleractinians. In conformity with scleractinian usage, we have orientated the presumed dorsal pole uppermost in the material described here. However, we are not aware of relative acceleration in the pair of opposite sextants in scleractinians.



TEXT-FIG. 4. A, *Kilbuchophyllia discoidea* gen. et sp. nov. Idealized reconstruction of septal pattern. Plane of bilateral symmetry vertical with supposed dorsal pole uppermost. B, *Fungiacyathus symmetricus* (Pourtalès). BM(NH)Z 1880.11.25.123, Recent specimen, collection station details uncertain, $\times 4$.

The distinctive pattern of nested triads of second and higher orders of septa is similar to a version of Portalès Plan which is developed in some scleractinian corals. Pourtalès Plan is regarded as a reflection of septal substitution during ontogeny, when the peripheral ends of exosepta split to accommodate subsequent entosepta. Vaughan and Wells (1943, p. 34) stated that it may be assumed that substitution has occurred when septa of a higher cycle unite with those of a lower cycle. A range of patterns of uniting septal ends is possible in detail, but the arrangement in the present material is remarkably similar to that exhibited by such Scleractinia as *Fungiacyathus symmetricus* (Text-fig. 4B; Vaughan and Wells 1943, pl. 34, figs 1a and 4) and *Balanophyllia (Eupsammia) zelandiae* (Squires 1958, p. 73, fig. 28). However, this is not identical to the classic pattern in dendrophyllid corals illustrated by Vaughan and Wells (1943, fig. 13) and Wells (1956, fig. 239) in which the entosepta are less well-developed than the exosepta. Also the pattern in the present material is equivocal. The axial septum of a triad is usually more or less structurally continuous and the flanking septa bend towards but do not always touch or merge with the axial septum. This does not immediately suggest the process of substitution. In some cases the peripheral ends of existing septa are deflected around the tips of newly inserted septa, at this stage a string of septal spines, in a manner suggesting substitution. However, we cannot be certain that these instances are not irregularities in insertion rather than clues to its character. If septal splitting did occur, the appearance of septa in the smaller specimens suggests that it was unlikely to have affected either the first or second orders. It seems also that further work is needed on the origin of some of the patterns attributed to Pourtalès Plan in living corals. Thus it is premature to claim septal substitution as occurring in this Ordovician material.

This very close similarity to the Scleractinia is reflected in other features. The origination of septa as discrete spines, subsequently linked by thin blades of material to give a beaded appearance to the septa, is very reminiscent of the early stages of skeletal development in some Recent corals (see, for example, Jell 1980). The rather confused appearance and irregularities in metasepta insertion in the early ontogenetic stages mentioned and illustrated by Jell are very similar to those seen here. Furthermore, the coarsely denticulate upper margins of the septal blades in mature coralla are also

closely comparable to those seen in many scleractinian corals but are not a characteristic of the Rugosa. An epitheca or holotheca is almost universal among rugose corals but, as a well developed feature, is confined largely to some ahermatypic (mainly caryophyllid and dendrophyllid) forms among the Scleractinia. In the Rugosa and Tabulata, it appears always to develop from an initial conical structure secreted by the polyp on settlement and metamorphosis, whereas in the Scleractinia it develops on the edge of the basal disc (Jell 1980). In the present material the central area of the epitheca is featureless and flat; there is no sign of a conical stage in development (Text-fig. 2D,E). The microarchitecture of the epitheca shows similarities with that described for *Manicina* by Sorauf (1972), although the structures preserved here are much coarser in scale. Also, the character of the upper surface conforms closely in appearance to the secondary layer on the surface of the basal disc of *Porites lutea* illustrated by Jell (1980).

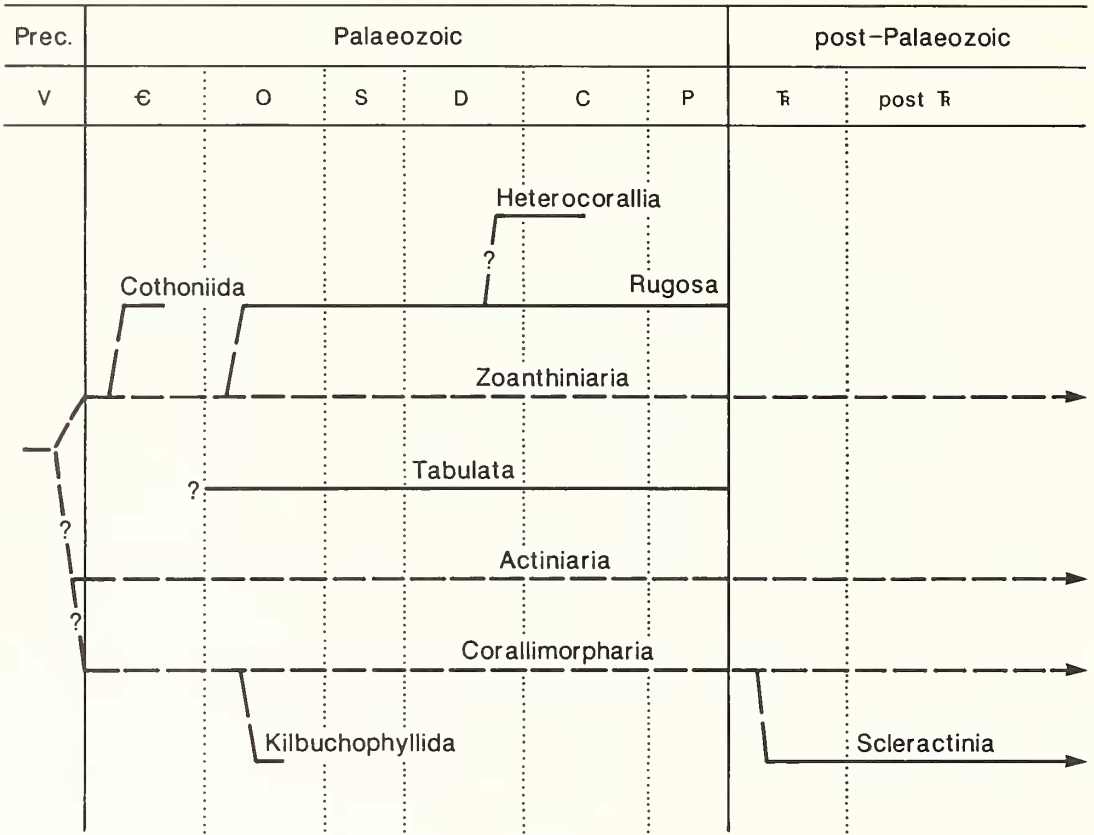
These specimens occur with a rich invertebrate fauna, preserved almost exclusively as moulds, the vast majority of which originally had calcium carbonate shells or skeletons. The skeletal material is thus assumed to have been calcium carbonate. Whether the skeleton was originally calcitic or aragonitic is much more speculative. Little is known of microarchitecture in the rugose corals, widely regarded to have been originally calcitic (Sandberg 1984), although internal ultrastructure appears to be identical to that in the Scleractinia. Sorauf (1980, p. 335) considered that biomineralization in the Rugosa closely resembled that in the Scleractinia, differing only in original mineralogy. In any case, in the material described here the finest detail of the microarchitecture is not preserved. The only evidence is indirect; similarity to the Scleractinia is so close that the original mineralogy may well have been the same, that is to say aragonitic.

Phylogenetic relationships

The evidence suggests very close affinity between this Ordovician material and the Scleractinia among the Zoantharia Anthozoa. It seems highly improbable that intermediates over a period of 220 Ma could all have escaped preservation and/or detection even if it is assumed that these corals remained ecologically confined to oceanic environments. In fact the associated organisms clearly indicate a shelf and/or upper slope fauna. It seems more probable that the Palaeozoic specimens represent an earlier, ultimately unsuccessful attempt at skeletonization by the same group of anemones that later gave rise, probably polyphyletically, to the Scleractinia. Such a conclusion requires the existence of anemones with a cyclic hexamerous pattern of mesenterial insertion at least as early as the mid-Ordovician. Thus it strongly supports the rejection of the Rugosa as ancestral to the Scleractinia (Oliver 1980).

The ancestral anemone group is usually considered to be the Corallimorpharia, identical to scleractinian polyps but skeletonless (Wells and Hill 1956; Hill 1981; Oliver and Coates 1987), although Hand (1966) has suggested the possibility of the reverse relationship on functional grounds, with the Corallimorpharia and Actiniaria evolved from the Scleractinia by loss of the skeleton. The new Ordovician material, however, appears to favour the former scenario. Furthermore, if its septal pattern can be confirmed to be identical to one known to result from septal substitution in living corals, this isolated skeletonized species would itself presumably require an anemone precursor already possessing paired mesenteries. Thus the range of the Corallimorpharia, and/or the closely related Actiniaria, must be extended back at least that far to provide the same ancestral anemone stock for this and the Scleractinia. Anemones have an almost non-existent fossil record (Scrutton 1979) but it now seems possible that all the various groups of anemones may have differentiated during the initial cnidarian radiation in the late Precambrian.

A possible phylogeny for the Palaeozoic Zoantharia Anthozoa, modified after that of Oliver and Coates (1987), is given in Text-figure 5. The present material has the same relationship to the Scleractinia as the Middle Cambrian Cothoniida probably, but perhaps less certainly, has to the Rugosa (Jell and Jell 1976; Scrutton 1979; Oliver and Coates 1987). The latter are regarded as having evolved from the Zoanthiniaria, in which later mesenterial couples are inserted serially in only one pair of sextants (Wells and Hill 1956; Hill 1981). The relationships of the other major group of Palaeozoic corals, the Tabulata (taken to include the Heliolitida) is equivocal. Some or all



TEXT-FIG. 5. Phylogeny of the Anthozoa Zoantharia (modified after Oliver and Coates 1987).

Rugosa have been claimed to have direct tabulate ancestry (Flower 1961) but, although the earliest skeletal ontogenetic stage appears always to be conical as in the Rugosa, we regard this as most unlikely (Scrutton 1979; Neuman 1984). Septa are absent or weakly developed in the Tabulata and no general pattern of insertion has been demonstrated. Tabulate corallites rather seldom show bilateral symmetry; septal development is usually radially uniform and 12 septa are sufficiently common, together with a rare instance of preservation of twelve tentacled favositid polyps, for a fundamental dodecal symmetry to have been claimed for the group (Copper 1985; Mistiaen 1989). These factors suggest a corallimorpharian or actiniarian ancestor to be as, if not more, likely for this group than a zoanthiniarian ancestor among known orders of anemones, although it seems equally possible that the tabulates evolved from a separate group of anemones now extinct.

SYSTEMATIC PALAEONTOLOGY

- Phylum CNIDARIA Hatschek, 1888
- Class ANTHOZOA Ehrenberg, 1834
- Subclass ZOANTHARIA de Blainville, 1830
- Order KILBUCHOPHYLLIDA nov.

Diagnosis. As for genus.

Discussion. The Kilbuchophyllida is homoeomorphic to a high degree with the Scleractinia. However, the combination of a solitary discoidal, epithecate form lacking dissepiments, with solid, bladed septa nested in triads and more or less strongly accelerated in the lateral sextants, does not appear to occur among the Mesozoic to Cenozoic scleractinian corals. Although the combination of characters in the only known species is unique, all, with the possible exception of the pattern of septal acceleration, are individually or severally found in various scleractinians. Ultimately, the classification of this species in a new order is based on its stratigraphic separation and our presumption of lack of direct descent to the Scleractinia.

Family KILBUCHOPHYLLIDAE nov.

Diagnosis. As for genus.

Genus KILBUCHOPHYLLIA gen. nov.

Derivation of name. After the type locality, Kilbucho (pron. -bukko), near Biggar, southern Scotland.

Diagnosis. Solitary, discoidal, epithecate radiobilateral corals showing hexamerous, cyclic septal insertion. Septa, spinose to solid blades, arranged in a pattern with the internal ends of higher order septa turned towards or resting against the flanks of lower order septa. Adjacent sextants (?ventral pole) with retarded septal insertion in early ontogeny, lateral sextants accelerated in later ontogeny. No dissepiments.

Kilbuchophyllia discoidea sp. nov.

Plate 1, figs 1–8; Text-figs 2, 3, 4A, 6

Diagnosis. Circular, solitary, discoidal corals with diameter up to 28 mm and estimated maximum 120 septa. Up to six cycles of septa of which the fourth sometimes and the fifth and sixth cycles always are incomplete. Second and higher orders involved in pattern of nested triads. Insertion retarded in adjacent (?ventral) sextants in early ontogeny, accelerated in lateral sextants in later ontogeny. Axial area with discrete trabeculae (?pali) merging to form papillose or contorted axial structure. Weak bilateral symmetry usually apparent. Epitheca a flat disc with concentric growth ridges and occasionally septal grooves. No dissepiments.

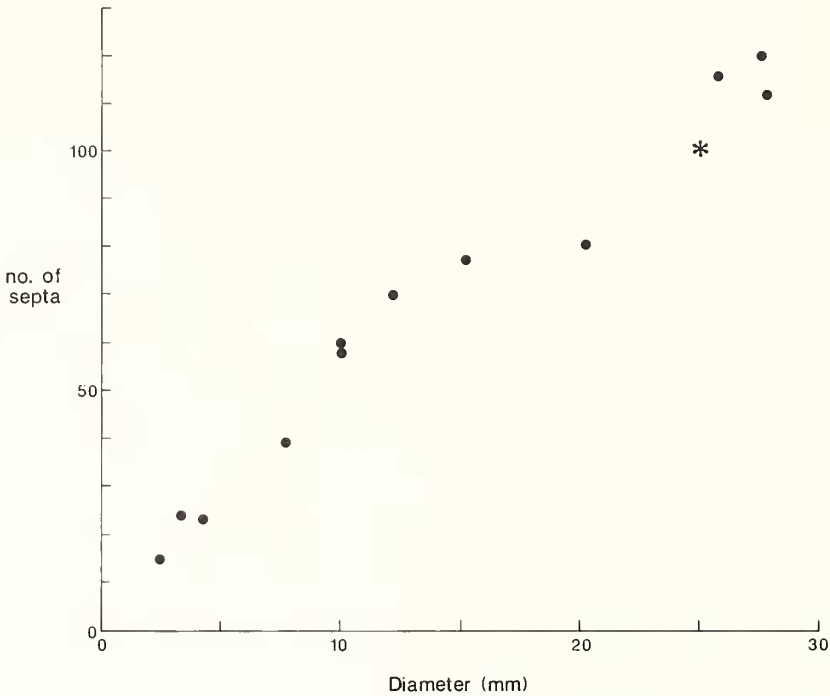
Holotype. RMS 1989.36.1. Ordovician, middle Caradoc; Kilbucho, near Biggar, southern Scotland.

Paratypes. RMS 1989.36.2–12; BGS 9936. Same horizon and locality as holotype.

Description. Solitary, circular, discoidal corals ranging from 2.6 mm diameter with 15 septa to 27.5 mm with estimated 120 septa (Text-fig. 6). In small coralla, septa either discrete trabecular spines or in lower order septa, spines linked by a low thin ridge giving septa a beaded appearance. In larger coralla, spines subsumed in smooth faced blades, c. 0.3 mm thick, with coarsely toothed upper margin in all but highest order septa, although less completely fused peripherally and particularly adaxially. Individual spines c. 0.2 mm diameter with axes c. 0.3 mm apart; septal teeth spaced c. 0.7–0.9 mm. Height of spines or septal blades 0.75–1.0 mm in smaller coralla, rising to c. 2.3 mm high in the largest coralla. Septal height greatest at mid length of smaller coralla, migrating to axial end of septa in larger coralla. Six first (protosepta) and six second cycle septa of more or less equal length, 0.8 radius in all but smallest coralla. Higher cycles, up to sixth, successively shorter in length. Second and higher cycles of septa involved in a pattern of nested triads, with higher cycles at their inner ends turned towards or resting against the flanks of lower cycles. The first two cycles complete in smallest available corallum, third cycle complete between 3–4 mm diameter, fourth cycle complete by about 10 mm, fifth cycle absent from smaller coralla, ?complete in largest coralla, sixth cycle variably present only in largest coralla and never complete. Septal insertion retarded in adjacent sextants (at ?ventral pole of polyp) in early ontogeny, accelerated in lateral sextants about plane of bilateral symmetry in later ontogeny. Axial area with

discrete trabecular spines, ?equivalent to pali, in smallest coralla. With size increase, spine bases variably embedded to form flat or slightly arched papillose area. In one case, spines linked as extensions of septa to form dome of twisted, interlocked plates. Bilateral symmetry may be weakly defined by a more or less well-developed bladed element in axis but sometimes not obvious. Epitheca a flat disc with peripheral depth 0.3–0.5 mm high. Central area featureless and may be almost smooth throughout but concentric growth ridges usually and radiating septal grooves sometimes clearly developed around central area. There are no dissepiments.

Discussion. Except for the smallest specimens, all the material is elliptical in plan. When apparent, the plane of bilateral symmetry is not coincident with the long axis of the ellipse and the shape is due to tectonic distortion in the rock. Strain analysis yields a value of R_1 of 1.06. Allowing for the difficulty of measuring axes accurately in some of the material, this suggests that the coral was originally effectively circular.



TEXT-FIG. 6. *Kilbuchophyllia discoidea* gen. et sp. nov. Plot of septal number against diameter for better preserved material. Both parameters estimated in many cases because of damage to margins of specimens. Holotype indicated by asterisk.

Variation in most features in the material available, allowing for ontogenetic stage, is relatively limited. The axial structure is the most variable aspect of mature specimens. One coral, BGS 9936, representing an early ontogenetic stage, is unique in possessing a distinct low rim linking the peripheral ends of septa. Whether or not this is aberrant, or the rim is obscured by thickening of the upper surface of the epitheca in larger coralla, is unknown.

The specimens often appear to have suffered some damage before final burial, consistent with their presence in a debris flow. In particular, the septal blades in the larger specimens are often damaged and their upper margins incomplete. Because of incomplete preservation there is an

element of estimate in all the data on Text-figure 6, although the error is considered unlikely to exceed 10%.

Range. This species is known so far from some 20 specimens and fragments from the type locality. Two fragments have been recovered from similar beds of the same age at Wallace's Cast, Wandel Burn, 12 km west-south-west along strike, southern Scotland.

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